Content

1. Preface

The demand for forest products is increasing because of a growing world population and the transition from fossil to non-fossil fuels. Intensive forest management with fertilising of young forest has proven large possibilities in increasing the production of biomass in the tree-layer. The long-term effects of this kind of management on the environment are largely unknown. However, studies of traditional nitrogen addition in older forests may provide a useful background for understanding the dynamics in young fertilised stands. This literature review is written as an introduction to my PhD-studies and aiming at compiling present knowledge about vegetational changes in forests after addition of nitrogen. Jörg Brunet, Johan Bergh and Annika Nordin have given valuable comments on the manuscript. Małgorzata Blicharska provided the photos.

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2. Abstract

Most studies dealing with the effects on the ecosystem of nitrogen fertilisation or deposition show changes in the field and bottom layer vegetation of forests. According to some studies even low levels of added nitrogen result in changes in the field-layer vegetation. Effects of added nitrogen on vegetation can be divided into immediate and long-term effects. The immediate effects are caused by the toxicity of nitrogen on plants, especially bryophytes and lichens. The long-term effects are likely an effect of an accumulation of nitrogen in the system, through increased competition in the ground vegetation and decreased insolation due to a closing canopy. Ecosystem changes are dependent on several preconditions, such as: initial composition of the vegetation, initial nutrient status and light conditions. In general tall and fast growing species are favoured by addition of nitrogen, while species less responsive to increased levels of nitrogen in terms of increased growth are disfavoured. Species which can utilise nitrate through enhanced nitrate-reductase activity are promoted. In some vegetation types the interference of pathogens has been shown to mediate the change in vegetation. The species richness of a site is to large extent determined by other factors than availability of nutrients, like soil acidity. Many bryophytes and lichens decrease in abundance as an effect of increased levels of nitrogen. A plausible explanation is their low growth potential. A few studies on the activity of cyanobacteria associated with bryophytes and lichens have shown a significant decrease in activity when nitrogen was added to the site. Many studies indicate that competition between strata (e.g. from the tree canopy) is essential for the response in ground vegetation when a forest is fertilised.

3. Introduction

The demand on increased forest production has rapidly increased, since there is a great need to replace fossil fuel by forest products, which can be used for bio-energy purposes. The global climate change due to emissions of gases like CO_2, CH_4 and N_2O enforces a transition from fossil fuels to alternative energy sources. Energy from biomass is one of the solutions discussed. The forest industry is traditionally dependent on a production of pulp, paper and sawn timber. The share of biomass-originated energy carriers in the production is however increasing and the forest industry is concerned about the future supply of raw-material. There is also an increased demand from the forest industry in Sweden and the demand-supply situation has been even more severe as an effect of increased restrictions to import forest products from Russia. The land available for agricultural and forest production, decreases because of increased demand by the society for other land-uses. Examples are areas for protection of biodiversity, recreation, construction and infrastructure. At the same time the demand for biomass is increasing caused by an increased world population and raised welfare in many parts of the world. The pressure on the ecosystems to produce increased amounts of biomass is thereby both on the global and sector level.

Boreal and boreo-nemoral ecosystems are usually nitrogen limited (Tamm 1991). Nitrogen limited ecosystems can be defined as those where the primary production markedly increases if a nitrogen fertiliser is supplied (Tamm 1991). The total storage of nitrogen in the upper layers of the soil is however, usually large as an effect of slow mineralisation processes (Lundmark 1986). Nordic long-term experiments on how the forest production is effected by fertilisation show a drastic increase in biomass production and that the actual production today is less than the potential production (Bergh 2000).

Today most fertilising of forest land in Sweden is performed as a N-supply at a single or a few occasions, normally in the end of the forests rotation period and with about 15 g m^{-1} of nitrogen per occasion (Nohrstedt 1998; Nohlgren & Nohrstedt 1995; Kellner 1993b;). There is a growing interest of introducing more intensive fertilisation programs in Norway spruce stands with its highest intensity in young stands, until the stand reaches a closed canopy. In this type of fertilisation programs a balanced supply of fertiliser is given, which is based on nutrient analysis of needles. Field experiments with a balanced nutrient supply have shown an increased stem wood production by 50 to 250 per cent in southern Sweden and northern Sweden (Albrektson et al. 1977; Axelsson & Axelsson 1986; Bergh 2000; Bergh et al. 1999).

There is however environmental concern associated with the introduction of intensive forest management. Most plants in northern-central Europe are adapted to ecosystems limited by nitrogen. According to Ellenberg (1988), as many as 50 per cent of the plants species are only competitive on nitrogen poor sites. Young coniferous forests are in general more trivial than mature when it comes to composition of the flora and fauna (Elofsson & Gustafsson 2000). As the stand grows mature the number of niches increase and species can colonise/recolonise. In intensive forestry, the rotation periods are in general shorter (Bergh 2000). By introducing intensive forest management on a broad scale, the share of forest in the old phase will decrease. Thereby there is a risk of habitat fragmentation due to habitat loss and isolation.

This literature review will concentrate on the effects of fertilising on ground vegetation in boreal and boreo-nemoral coniferous forest. As an effect of similarities between fertilising and anthropogenic deposition, the review includes studies with both approaches.

4. Production of biomass

The response of a certain ecosystem to an increase in nutrient availability varies due to the initial fertility of the site and the present species composition. When comparing species adapted to different nutrient availability, species adapted to high levels of nutrients usually react by increased production to a larger extent compared with species which grows on less fertile soils. However, when comparing individuals of the same species, those growing on less fertile sites usually increase production the most, when nutrient availability increases (Chapin et al. 1986).

Studies on the effects on the ground vegetation from addition of nitrogen, either in experiments studying the effects of anthropogenic deposition or fertilisation of forest as a silvicultural measure, very often showed changes in production of biomass of certain species as a response to added nitrogen (Parsons et al. 1994; Aerts et al. 1990; Aerts 1989; Albrektsson et al. 1977; Persson 1981; Tilman 1984).In some cases, however, no significant change in production of biomass was observed (Nordin et al. 1998). According to Albrektsson et al. (1977) the total biomass production in the field-layer increased slightly, while there was a marked change in species composition. These results are partly consistent with Press et al. (1998) who however did not notice any change in total biomass, but an altered composition. A decrease in bottom-layer species was compensated by an increase in the field-layer. Mäkipää (1994) found that the total biomass of bryophytes decreased on all types of sites when fertilised, while lichens decreased in biomass on dry sites. A slight increase of biomass in grasses did not compensate for the decrease in mosses and the total change of the biomass of the ground vegetation was negative. These results are supported by another study by Mäkipää (1998b), where the effect of ammonium sulphate on ground vegetation was studied. Here the biomass of bryophytes decreased significantly during the four year study period, while changes in vascular plants were insignificant.

The total production of the ground vegetation under a fertilisation regime is difficult to forecast. In short term studies of biomass production in boreal plant communities, which often are dominated by dwarf shrubs, an increased production may be masked by the large amount of living biomass. Parsons et al. (1994) did not notice any change in total above-ground biomass as an effect of fertilisation, even though many parameters of growth increased. This was probably because of a large initial biomass which masked the changes. A total increase in production may in many cases, where the dominating species are occurring on the edge of their nutritional niche, require a change of species (Chapin et al. 1986). To fully understand the change in productivity of an ecosystem under addition of nitrogen, changes in allocation between different strata should be taken into account.

5. Species richness

Kellner and Redbo-Torstensson (1995) compiled information from literature about species richness in relation to deposition of nitrogen. Out of six scrutinised publications, three reported an increase in species, in one there was no change and two did not give any information about number of species. Two of these studies were performed in Fennoscandia, which either did not give any information about number of species or did not show any change. Results from fertilisation experiments by Kellner (1993a) in coniferous boreal forest in Sweden did not reveal any significant change in number of species by addition of nitrogen. There was, however, a positive relation between species replacement and fertilisation. In the fertilised plots the number of plants, which were not present in the control plot, increased with the fertiliser dose. An unaffected number of species was also noted from an experiment in southern Sweden, where deposition of nitrogen was simulated (Hallbäcken & Zhang 1998). VanderSchaaf et al. (2000) did not find any consistent trend in the reaction of plant diversity to fertilisation in five experiments in northwest USA.

Press et al. (1998) found that both species richness and Shannon's diversity index decreased due to fertilisation. This was a result of a decreased number of bryophytes and lichens. Bobbink et al. (1998) predicted that increased levels of nitrogen may lead to loss of diversity on sites with intermediate nutrient availability caused by an increase of competitive plants. These results are supported by Thomas et al. (1999) who found a decrease in species number in fertilised *Pseudotsuga menziesii* forest in Washington State (USA). On the other hand, Bobbink et al. (1998) suggest a possible increase in species number on nutrient-poor sites due to immigration of species that were not adapted to the initial nutrient status.

There are several factors, besides fertility which determine the species richness of a site. Examples are soil acidity, availability of water, light conditions and historic land-use. There is a positive relation between pH in the soil and species richness in old coniferous forests in central Sweden (Helliwell 1975) and in *Quercus/Carpinus* forests in southern Sweden (Tyler 1989). In the study by Tyler (1989) soil pH was most important for species richness at low to mediate canopy cover. VanderSchaaf et al. (2000) claimed that the initial composition determines the effects of fertilisation according to the following statements:

1. If most species in the plant community respond relatively similar to treatment, then diversity may be unchanged even though total biomass increase may be large.
2. If a highly responsive species is abundant prior to the treatment, then diversity may decrease following fertilisation.
3. If highly responsive species are relatively rare prior to treatment, then diversity may increase following fertilisation.

The often detrimental effects of fertilising on bryophytes and lichens (see chapter 7 and 8) make the initial richness and composition of these communities important for the

outcome on species richness of added nitrogen. It also put demands on the design of research. These species are often difficult to determine in the field why it may be tempting to group species. That way a lot of information can be lost. The effects of changes in nutrient properties of the soil on species richness can be expected to be dependent of position in the landscape and elapsed time.

6. Vascular plants

The very common boreal and boreo-nemoral vegetation type, dominated by dwarf-shrubs like *Calluna vulgaris, Vaccinium myrtillus* and *V. vitis-idaea*, are commonly noted to decrease in cover when an ecosystem is exposed to increased levels of nitrogen (Strengbom & Nordin 2008). The reaction of these dwarf shrubs are however not consistent and examples of the opposite have been reported. Forbs and grasses are in general dominating among plants that are favoured by nitrogen (Press et al. 1998; Nams et al. 1992; Gerhardt & Kellner 1986; Guzikowa et al. 1976). Frequently *Deschampsia flexuosa* (Kellner & Redbo-Torstensson 1995) increases together with *Rubus idaeus* and *Epilobium angustifolium* (Strengbom & Nordin 2008). The increase of *E. angustifolium* as an effect of fertilisation is also supported by a study from north-western Canada (Turkington et al. 1998). A compilation of reactions to addition of nitrogen is shown in table 1.

Table 1. This table presents the change of abundance among some vascular plants under a fertilising regime. Seven articles were scrutinised by Falkengren-Grerup et al. (2000). The numbers present the percentage of articles in which a species increased (+) or decreased (-).

+100	+80 to +40	+40 to -40	-40 to -80	-100
Athyrium filix-femina	*Deschampsia flexuosa*	*Anemone nemorosa*	*Linnaea borealis*	*Rubus saxatilis*
Rubus idaeus	*Epilobium angustifolium*	*Convallaria majalis*	*Luzula pilosa*	
	Trientalis europaea	*Dryopteris expansa*	*Vaccinium myrtillus*	
		Gymnocarpium dryopteris	*Vaccinium vitis-idaea*	
		Lycopodium annotinum		
		Maianthemum bifolium		
		Melampyrum pratense		
		Orthilia secunda		
		Oxalis acetosella		
		Thelypteris phegopteris		

There seems, however, to be differences in the reaction to nitrogen due to the initial fertility of the site. Kellner (1993a) found that the response of *Vaccinium* species to fertilisation differed with site fertility. While the *Vaccinium* species decreased on more fertile sites, no change or even an increase was noted on the poor sites. This is supported by the results of Persson (1981) who found that *V. vitis-idaea* increased by

fertilisation on a site, which initially was dominated by *C. vulgaris* and *V. vitis-idaea* in the field layer and lichens in the bottom layer. A similar pattern was found by Mäkipää (1994). In her study the *Vaccinium* species decreased on mesic sites while *V. vitis-idaea* increased on dry sites. On a lichen-rich site, *C. vulgaris* increased significantly by fertilisation (Eriksson & Raunistola 1993), while no significant changes at all were found concerning vascular plants after fertilisation of a sandy soil in Norway (Skrindo & Økland 2002). In general dwarf-shrubs seem to be disfavoured by nitrogen fertilisation. Some studies have however not been able to detect any change (*V. myrtillus and V. vitis-idaea*; Nohrstedt 1998; *Arctostaphylos uva-ursi*; Nams et al. 1992) and some an increase (*Empetrum hermaphroditum*, *V. myrtillus, V. uligonosum and V. vitis-idaea*; Parsons et al. 1994). The traits of plants favoured or disfavoured are treated in chapter 9-11.

Forest field layer vegetation with *C. vulgaris*, *V. myrtillus* and *V. vitis-idaea*.

The way vegetation changes because of an altered nutritional status depend as mentioned above on a multitude of factors affecting the competiveness of different plants. There is inertia in the change of vegetation caused by altered nutritional status of the ecosystem. The composition of the initial on-site vegetation decides the immediate alteration. The more long-term effects are however controlled by several other factors, including the vegetational composition in the surrounding landscape. Available diaspore sources are important, as well as rate of dispersal, available dispersal agents and factors affecting success of establishment.

7. Lichens

Lichens seem to be very sensitive to addition of nitrogen. Several studies on fertilisation and deposition of nitrogen have shown negative effects on lichens (Strengbom & Nordin 2008; Skrindo & Økland 2002; Nohrstedt 1998; Press et al. 1998; Turkington et al. 1998; Mäkipää 1994; Nohrstedt 1994; Eriksson & Raunistola 1993; Nohrstedt et al. 1988; Kellner 1993a; Gerhardt & Kellner 1986; Persson 1981). However, species from the genus *Cladonia* (species belonging to both *Cladina* and *Cladonia* according to presently utilised nomenclature) increased initially in the study by Persson (1981) when fertilisation was combined with irrigation. The author characterised these species as pioneer species, e.g. species with a good ability of colonisation but with low persistence. It is possible that lichens were restricted by the low supply of water and nutrients prior to the fertilisation and thereby did not utilise the total spatial niche. The long-term effects on lichens are also very pronounced. For example Olsson and Kellner

(2006) showed an up to 50 per cent reduction in the cover of *Cladina rangiferina*, 15-18 years after fertilisation with a total dose of 1000 kg N ha^{-1}.

Forest bottom layer vegetation. Mixed lichen-bryophyte society.

There is probably a combination of factors behind the decline of lichens in fertilisation experiments. One explanation often mentioned in the literature is the lack of cuticle in lichens. This can make these species more sensitive to increased levels of salts in the environment. This can not, however, explain the long term effects of fertilisation on lichens (se also chapter 12). Lichens with associated cyanobacteria have been noted to survive damages from fertilisers of up to 90 per cent of the individual (Nohrstedt et al. 1988). Cyanolichens are strong competitors on less fertile sites because of the ability of the associated bacteria to fixate nitrogen. Addition on nitrogen has shown to be negative to the nitrogen fixing activity of cyanobacteria. DeLuca et al. (2008) found a negative relationship between throughfall of nitrogen and nitrogen fixing activity on cyanobacteria on pleurocarpous feather mosses in the boreal part of Sweden. If these results also are applicable on cyanobacteria in lichens, which is indicated by Nohrstedt et al. (1988), this could be one of the contributory factors behind the decline of lichens in fertilisation experiments.

Lichens also lack the possibility to react by height growth to changes in the environment, like increased nutrient availability or decreasing amount of light, and are thereby less competitive. In addition, cyanolichens are species which in general require much light. Fertilisation of coniferous forest increases rapidly needle biomass and eventually the amount of litter (Albreksson et al. 1977). Mäkipää (1994) found that the humus layer increased with 14 to 115 per cent as an effect of fertilisation. A closing canopy, both in the field layer and the bottom layer together with increased amounts of litter can be expected to disfavour lichens.

8. Bryophytes

Many bryophytes in southern Sweden have been noticed to decrease due to pollution from sulphur and nitrogen. Many species which were frequent in Scania before, now only occur in refuge areas (Hallingbäck 1992). The species in the study were mostly epiphytic, while the focus in this literature review is on epigeic species. In relation to lichens the effects of fertilisation on bryophytes appear to be more inconsistent. There are differences between species in competitive abilities when nutrient conditions are altered. Consistent in most studies is that species common in the bottom layer of boreal and boreo-nemoral coniferous forests like *Dicranum fuscescens*, *D. polysetum*, *Hylocomium splendens* and *Pleurozium schreberi*, seem to decline due to increased levels of nitrogen. On the other hand species in the genus *Brachythecium* and

Plagiothecium appear to react consistently positive to fertilisation (Strengbom & Nordin 2008; Olsson & Kellner 2006; Skrindo & Økland 2002; Van Dobben et al. 1999; Hallbäcken & Zhang 1998; Press et al. 1998; Andersson et al. 1995; Kellner 1993b; Dirkse & Martakis 1992; Gerhardt & Kellner 1986). The results of Hallbäcken and Zhang (1998) are, however, not consistent with the other studies, here no effect was detected on *P. schreberi.* Bryophytes that have been found to respond either positively or negatively are presented in table 2.

Table 2. Schematic response to fertilisation and deposition of some bryophytes, after Dirkse & Martakis (1992). Substrate preferences according to Hallingbäck (1996) and Hallingbäck & Holmåsen (1985). A frequent substrate is indicated by"+", a less frequent substrate is indicated by "(+)". Indicator values and life form from Ellenberg et al. (2001). An X is indicating an indifferent or very varied behaviour. Light: occurrence in relation to relative irradiance intensity, 1 = deep shade → 9 = full light. Temperature: occurrence in the temperature gradients from the Arctic and the Mediterranean and from Alpine levels to lowland, 1 = extremely cold conditions → 9 = extremely warm conditions. Continentality: occurrence in the gradient from the Atlantic coast to the inner parts of Eurasia, 1 = extremely oceanic → 9 = extremely continental. Moisture: occurrence in the gradient from dry to swampy ground, 1 = extreme dryness → 9 = wet sites. Reaction: occurrence in the gradient of soil acidity and lime content, 1 = extreme acidity → 9 = basic reaction and lime. Life forms, C: chamaephyte hibernating on the substrate, H: hemicryptophyte, hibernating buds near the soil surface, E: epiphyte, growing on living plants. For a more comprehensive explanation of the indicator values and life forms, see Ellenberg et al. (2001).

		Substrate									**Indicator value**					
Species	**Effect of treat-ment**	*bark*	*humus*	*litter*	*peat*	*rock*	*roots*	*sand*	*soil*	*decaying wood*	*Light*	*Temperature*	*Continentality*	*Moisture*	*Reaction*	*Life form*
Brachythecium oedipodium	+			+						+	3	4	7	6	3	E, C
Brachythecium reflexum	+	+		+		+			+		4	2	6	5	4	C (E)
Brachythecium starkei	+	+		+		(+)	+			+	6	1	6	6	2	C (E)
Lophocolea heterophylla	+									+	4	3	5	4	3	C,H,E
Plagiothecium denticulatum	+					+			+	+	5	X	5	4	5	H
Plagiothecium laetum	+					(+)				+	4	3	6	4	2	H (E)
Pohlia nutans	+	+		+	+			(+)	+	+	5	X	5	4	2	C
Polytrichum formosum	+					+					7	3	5	5	2	H
Polytrichum longisetum	+				+						8	2	6	7	2	H
Dicranum fuscescens	-	+				+				+	7	2	6	6	2	C
Dicranum polysetum	-		+	+		+		+			6	3	6	4	5	C
Hylocomium splendens	-			+		+			+		6	3	6	4	5	C (E)
Pleurozium schreberi	-			+		+			+		6	3	5	4	2	C
Polytrichum commune	-				+						6	2	5	7	2	H
Polytrichum juniperum	-				+				+		8	2	5	4	3	H
Ptilidium ciliare	-			+		+			+		8	3	6	4	2	C

In a study by Turkington et al. (1998) in north-western Canada the total biomass of bryophytes decreased due to fertilisation, which is supported by Mäkippää (1994, 1998b). The study by Turkington et al. (1998) did not separate between different species

and in the experiment by Mäkipää (1998b) the treatments were conducted with ammonium sulphate. Only one study in this review reports indifference of bryophyte's reaction to fertilisation. This study by Mälkönen et al. (1982) did, however, only last for two years after the application of NPK fertiliser. There may be differences in the effect of fertilisers on bryophytes by the way the fertiliser is applied. Persson (1981) found a significant increase of *P. schreberi* when the fertiliser was applied together with irrigation. Also *D. fuscescens, D. polysetum* and *H. splendens,* which in studies referred to above decline due to fertilisation, showed a greater abundance in the plots that were treated with both fertilisation and irrigation than in the control and the plots with only fertilisation. The effect in plots with only irrigation was weaker, although also here an increase of *P. schreberi* was found.

There appears to be few differences in preferences towards substrate between bryophytes which react positively or negatively to fertilisation (table 2). A larger share of species with a positive reaction seems however to utilise decaying wood. There is little consistency in traits between species with the same reaction to fertilising according to the indicator values and division into life forms (table 2) from Ellenberg et al. (2001). However, a somewhat larger tolerance to shade is indicated for the species with a positive reaction to fertilising. In a situation with increased competition for light due to an increased availability of nutrient such species can be expected to be more competitive than less shade-tolerant species.

Pleurozium schreberi.

Several authors suggest that the alteration of the bryophyte societies, by addition of nitrogen, is mainly owing to initial toxic effect (Mäkipää 1998a; Persson 1981; Turkington et al. 1998). Persson (1981) claimed that a gradual fertilising in water solution diminish this effect. The fact that bryophytes lack cuticle make them sensitive to increased levels of salt. This can, however, not explain the long-term effects on bryophytes, described in chapter 12, about recovery after ceased fertilisation/deposition. Initially the study area in Persson (1981) was dominated by lichens which indicate a dry site. The cover of *P. schreberi* was initially low, but present to a significant degree. Fertilisation together with irrigation could push the system in a direction were *P. schreberi* is more competitive. Bryophytes are low-growing species with minor ability to increase height growth if nutrient availability increased.

DeLuca et al. (2002) found that cyanobacteria associated with *P. schreberi* are N-fixing between 1.5 and 2.0 kg N ha^{-1} yr^{-1} in boreal forests and the system can be disturbed by

addition of nitrogen (see DeLuca et al. 2008 and discussion in chapter 7). Changes of the nutrient status in the system, and following alteration in competition both between and within strata, are of greater importance for the changes in bryophyte societies than toxic effects. There is however indications of enhanced effect of nitrogen in combination with sulphur (Hallbäcken & Zhang 1998). Sulphuric deposition might therefore be another factor of importance when considering the effects on bryophytes of added nitrogen.

9. Ammonium or nitrate

The competitiveness of different plants in a changed nutrient status with more available nitrogen differs depending on the ecology of the plants. In boreal ecosystems nitrogen in the soil is largely available as ammonium. The soils are often naturally acid since the mineral weathering of the bedrock produce acid materials. The activity of oxidising bacteria like *Nitrosomonas* and *Nitrobacter*, which transforms ammonium into nitrite and nitrate is usually limited by high soil acidity and strong competition for nitrogen in boreal forests (Tamm 1991). However, in acid forest soils bacteria of the genus *Nitrosospira*, which are more resistant to low pH, usually replace *Nitrosomonas*. This way the nitrification process is mostly limited by the supply of ammonium and can progress even at low pH (Eriksson et al. 2005).

Many of the common boreal plants are lacking the enzyme nitrate-reductase, which is essential for the plant to utilise nitrate-nitrogen. Plants like *V. myrtillus* and *V. vitis-idaea* almost lack this possibility. However, one of the most frequent grasses in this kind of environments, *D. flexuosa*, has proven the ability to reduce nitrate. In general the plant societies show a higher degree of this ability at higher fertility of the soil. *Urtica dioica,* a plant that is abundant on fertile sites, is one of the most efficient plants in reducing nitrate. The limiting factors for the nitrate-reductase are increasing temperature (the higher temperature, the lower reductase), light and availability of nitrate (Högbom 1992; Högbom & Högberg 1991; Högberg et al. 1990). Laboratory experiments with *V. myrtillus* and *V. vitis-idaea* have shown that these plants are able to grow in solutions with either ammonium or nitrate as the nitrogen source. The best performance in the sense of growth was though in solutions with only ammonium or a mix of ammonium and nitrate. In mixed solutions the relative uptake of ammonium was extending the uptake of nitrate (Ingestad 1973).

Both nitrite and nitrate has been proven to enhance the germination of dormant seeds (Hendricks & Taylorson 1974). However, Granström (1982) found mostly seeds of *V. myrtillus and L. pilosa* in the seed banks of a selection of forest sites in northern Sweden, even though for example *D. flexuosa* was frequent in the present vegetation. The low numbers of *D. flexuosa* seeds in the seed bank was confirmed by Hester et al. (1991), who found few *D. flexuosa* germinating from the soil even though this species was frequently represented in the seed rain. The most common species in this study were *C. vulgaris* and *Agrostis capillaris*, which indicate that these species are persistent in the seed bank. Species commonly found in seed banks are *C. vulgaris, L. pilosa* and *V. myrtillus*, which in most studies not are considered to be favoured by addition of nitrogen. Thereby the importance of nitrate and nitrite on the germination of seeds may be less important for the competition between plants after addition of nitrogen.

Since the nitrification is mainly limited by availability of ammonium the process is enhanced by fertilisation or deposition of nitrogen. Enrichment of nitrogen will therefore push the balance in a direction where a larger part of the available nitrogen consists of nitrate. A larger share of nitrate-nitrogen will in turn favour plants with nitrate-reductase. The limiting effects of deficient light on the nitrate reductase can be a factor explaining the lack of response to fertilisation in *D. flexuosa* described in chapter 10.

10. Competition for light and water

In a study of five deciduous tree species (*Acer rubrum, A. saccharum, Fraxinus americana, Prunus serotina* and *Quercus rubra*) in Canada the response in light absorption due to differences in availability of light and nutrients was tested. The spectral reflectance in the visible waveband increased due to increased light and decreased due to increased availability of nutrients. Subsequently, fertilisation increased the absorption of light. There are differences in ability of plant species to utilise nutrients to increase their absorption of light. This dissimilarity may be one explanation to why plants show different competitive abilities in a situation with increased levels of nutrients (Baltzer and Thomas 2005). The species *V. myrtillus* and *V. vitis-idaea* are used in Swedish forestry as indicators of different levels of fertility, with *V. myrtillus* growing on more fertile sites. Mäkipää (1999) did not, however, find any difference between the two species preferences to the availability of nitrogen. Both species showed similar Gaussian response curves along a nitrogen gradient and had almost the same nitrogen optima. These results suggest that other factors than the nutrient availability determines the competitive relation between the two dwarf-shrubs.

During the last decades the standing volume of *P. abies* forests in southern Sweden has increased. Since the studied species are light dependent this might influence their occurrence. Kardell and Eriksson (1990) showed a positive relationship between the biomass of *V. myrtillus* and the age of the forest. This indicates that in today's forestry, with shortened rotation periods, *V. myrtillus* is disfavoured. The intensity of logging activities has influence on the balance between *V. myrtillus* and species like *E. angustifolium* and grasses. Bergstedt and Milberg (2001) found in a study based on material from the Swedish National Forest Inventory that *V. myrtillus* decreased linearly with increased logging. In the same study *E. angustifolium* and grasses increased at very high logging intensities (e.g. when more than 80% of the forest cover was removed). Elemans (2004) studied response to different conditions in light and nutrients of four vascular plants; *Circaea lutetiana, Mercurialis perennis, Aegopodium podagraria* and *Impatiens parviflora*. The most important factor was light intensity, while nutrients only were important at higher levels of light. In a study by Strengbom et al. (2004) the enhancement of light in a fertilisation – light experiment showed a direct response by the increased growth of *D. flexuosa,* whereas the cover of *V. myrtillus* was reduced. There was no significant difference between the treatments with and without addition of nitrogen. This study lasted only one year. In a more long-term study it is possible that effects of nitrogen would also be detected.

Plant abilities to utilise increased levels of nutrients are to a large extent determined by their capacity to compete for other resources. Species that can utilise the surplus of

nutrients to increase height growth and specific leaf area (SLA) or are larger grown are better competitors. In a study by Knops and Reinhart (2000), of the reaction in SLA of three grass-species to increased levels of nitrogen, large differences between species were distinguished. The increase in SLA ranged between 28 and 82 per cent. This lead to a change in dominating species from *Poa pratense* to *Agropyron repens*. Diekmann and Falkengren-Grerup (2002) found that plants with the following traits increased most in abundance due to deposition of nitrogen.

- Tall stature
- Hydro- to helomorph anatomy
- High leaf concentration of nitrogen
- Late phenological development

A model introduced by Aerts and Van der Peijl (1993) added fast achievement of maximal biomass to the traits of nitrogen favoured plants. According to this model the slow-growing plants characteristic of nutrient-poor habitats can compete because of high maximum biomass.

Many studies have shown a positive growth response of trees through fertilisation (Bergh 2000). Fertilisation leads to increased growth of foliage and canopy closes and reduces the amount of light on the forest-floor. Competition for light in closed canopies decreases the effect of a nitrogen supply on the composition of the ground vegetation (Liljelund & Torstensson 1988). A denser canopy leads to a decreased number of plants in the field-layer (Bergstedt & Milberg 2001) and decreased total cover of the ground vegetation (Tyler 1989).

There are however considerable time-lags in the effects of added nitrogen on plants of the forest floor. Bergstedt and Milberg (2001) found that the effects of logging on plant community in the forest were most pronounced 7-11 seasons after the trees were cut. The changes in light after logging come more abrupt, compared with the effect on light conditions after fertilisation or deposition. Subsequently can even larger inertia in the effects of increased availability of nitrogen be expected. Eventually also the amount of litter from the trees increases, which can be negative to the ground vegetation. The effect of nitrogen addition on the biomass production in the ground vegetation is therefore to a large extent dependent on the competitiveness of the dominant tree species. One of the objectives with fertilisation of forests is to achieve a larger biomass of needles to sequentially increase the growth of the trees. A successful fertilisation of a forest is therefore inevitably leading to a greater competition from the tree-layer on the ground vegetation. The tree-layer is thereby determining whether or not and to what extent vegetation can exist on the forest floor (Tamm 1991). The importance of the tree-layer has also been stressed by Tyler (1989), who found light to be restricting especially among species tolerant to acid soils.

11. Response of pathogens to increased levels of nitrogen

It is hypothesised that exposure to increased levels of nitrogen will modify plants susceptibility to pathogens (Bobbink et al. 1998). Several studies on effects of fertilisation and anthropogenic deposition of nitrogen has shown increased pathogenic predisposition of *V. myrtillus*. The parasitic fungi *Podosphaera myrtillina* and *Valdensia heterodoxa* (Nordin et al. 1998; Strengbom et al. 2003; Strengbom et al. 2002) and the larvae of *Lepidoptera* (Nordin et al. 1998) increase their population growth when nitrogen is added to the ecosystem. *V. heterodoxa* causes brown spots on the leaves while *P. myrtillina* makes the leaves violet. Longevity of the leaves of *V. myrtillus* decreases because of both pathogens and is therefore a competitive disadvantage to its host plant. According to Nordin et al. (1998) *P. myrtillina* increased 10 and 60 times and *V. heterodoxa* 30 and 90 times, in treatments with N-addition of 25 and 50 kg N ha^{-1}. In the same study damages by larvae of *Lepidoptera* increased with a factor of 2 and 5, respectively. A decreased content of phenolics in leaves of fertilised *V. myrtillus*, was discovered by Witzell and Shevtsova (2004), and can be one explanation to the increased susceptibility to *V. heterodoxa*. In this study no significant changes were found at low levels of added nitrogen (12.5 kg ha^{-1} y^{-1}), while a high dose (50 kg ha^{-1} y^{-1}) decreased three out of five phenolics. However, when the most intensively fertilised plants where infected by the parasitical fungi, the levels of phenolics increased to ones comparable with unfertilised plants.

V. myrtillus infected by pathogenic fungi.

The suitability of *Calluna vulgaris* for the moth *Operophtera brumata* under addition of carbon dioxide and nitrogen was tested in an experiment in Great Britain. *O. brumata* is a polyphagous species known to be able to cause serious decline of *C. vulgaris* in moorlands of Scotland. The study did not reveal any relationships between enhanced levels of carbon dioxide and the development of *O. brumata*. There was however, a strong relationship between larval development, growth rate and pupal weight, and the addition of nitrogen. The phenolic content of the plants did not change. The authors suggest that the relationship between deposition of nitrogen and herbivory of *O. brumata* on *C. vulgaris* may be a key-factor behind the decline of moorlands in Scotland (Kerslake et al. 1998).

Experiences from laboratory experiments in the Netherlands show that the beetle *Lochmaea suturalis* which is monophagous on *C. vulgaris* increases its larval growth rate, adult weight and larval survival when feeding on *Calluna*-plants fertilised with nitrogen (Brunsting & Heil 1985). Several fertilising experiment in Dutch heathland show that only the addition of nitrogen to the system is not sufficient to initiate a vegetational change from heathland (*C. vulgaris*) to grassland (*D. flexuosa, Molinia*

caerulea). However, when *C. vulgaris* was removed or damaged by *L. suturalis*, factors like absence or presence of the grass species and nitrogen availability was correlated with the change in vegetation (Berdowski 1987; Aerts 1990).

The ecosystems in the studies above, heathland dominated by *C. vulgaris* and *Erica tetralix* completely or partly missing tree-layer, and boreal forest with a well developed tree-layer consisted of *Picea abies* and ground vegetation dominated by *V. myrtillus*, have some obvious dissimilarities. Despite this, both can be considered naturally nitrogen limited and similarities in the processes of vegetational change due to increased levels of nitrogen are evident. *L. suturalis* is present in all Fennoscandia (Fauna Europaea Web Service 2007). No studies have however, been done of how this species affects the interaction between *C. vulgaris* and grasses like *D. flexuosa* in the region. It is however reasonable to imagine similar behaviour of *L. suturalis* in northern ecosystems when exposed to high levels of nitrogen due to deposition or fertilisation.

As mentioned earlier in this literature review, different pathogens on for example *V. myrtillus* and *C. vulgaris* have shown to increase with addition of nitrogen. Strengbom et al. (2006) found a relation between the occurrences of *V. heterodoxa* on *V. myrtillus* and fertilisation with nitrogen in an experiment. The occurrence was, however, strongly related to scale in the sense of size of fertilised plots, where larger plots had larger incidence of decease. Large parts of Europe are affected by deposition of nitrogen. The deposition varies on a large scale due to sources of pollution and wind direction. However, the variation might be as large also on a landscape scale. Slopes and forest edges exposed to prevailing winds are likely to receive more deposition than other parts of the landscape (Hasselrot & Grennfelt 1987).

12. Recovery after ceased fertilisation/deposition

Fast recovery of some parameters like the chemistry of trees has been reported from fertilisation experiments in coniferous forest after the addition of nitrogen has ceased. Also levels of nitrogen in the soil-solution (Boxman et al. 1995), especially nitrate (Boxman et al. 1994) have shown to decrease relatively instant after ceased nitrogen fertilisation. The levels of nitrate reductase activity and nitrogen content in leaves of *D. flexuosa* have been shown to decrease relatively fast after fertilisation has ceased (Quist et al. 1999). Kellner (1993b) found a fast recovery of the vegetation after a single application of N. Initially *D. flexuosa* increased on the account of dwarf-shrubs like *V. myrtillus* and *V. vitis-idaea* on all sites. The effect peaked after two years and the vegetation started to recover.

A build-up of the total nitrogen storage in the system can however be expected. In a study by Ladanai et al. (2007), the total levels of nitrogen where still significantly enhanced 7-12 years after the fertilisation with NPK-fertiliser ceased. Strengbom and Nordin (2008) found a significant increase in total nitrogen content in *D. flexuosa* and *V. myrtillus*, 20 years after the last fertilisation. The effects of former land-use on soil properties have been reported to be persistent over long time periods. Falkengren-Grerup et al. (2006) found differences in soil N-content between previous agricultural land and land that had been continuously forested, 40-80 years after the agricultural land had been forested.

Some studies on the effect on the ground vegetation show remarkably long-lasting effects of increased levels of nitrogen in the system (Strengbom & Nordin 2008; Olsson & Kellner 2006; Strengbom et al. 2001). The most pronounced long-term effects have been noted in the composition and cover of bryophytes and lichens. Strengbom et al. (2001) found that reindeer lichens (*C. rangiferina* and *C. arbuscula*) present in the control plots still were absent in the plots were fertilising had ceased 9 years earlier. In the same study the bryophytes *B. starkei* and *P. denticulatum* were present only in the plots that had been fertilised, 47 years after the addition of nitrogen stopped. Simultaneously *H. splendens* was more abundant in the control plots. The considerable effects on lichens and bryophytes are supported by the results of Olsson and Kellner (2006) who studied the vegetation on sites where fertilisation ceased 15-18 years earlier (more about lichens and bryophytes in chapter 7-8).

The studies made of the long-term effects on vascular plants are however not consistent. While Strengbom et al. (2001) found significant effects on the relation *V. myrtillus – D. flexuosa* 9 years after the fertilisation had ended, there were no notable effects on vascular plants in the 47 years old experiment in the same study. The study by Olsson and Kellner (2006) of three fertilisation experiments, where the addition of nitrogen stopped 15-18 years earlier, did not show any increase in nitrophilic vascular plant species, neither did it show denser vegetation in the plots that were previously fertilised. Olsson & Kellner (2006) claim, that the long-term effects on lichens in their study had a stronger relationship with the accumulation of nitrogen in the soil, than with added nitrogen dose. Durable increase of system levels of nitrogen caused by fertilisation is also supported by Quist et al. (1999), who found a long-lasting increase of the nitrogen levels in leaves of *D. flexuosa*. Milchunas and Lauenroth (1995) reported nonlinear responses to ceased nitrogen enrichment of steppe communities. They hypothesized that litter accumulation as an effect of increased production and reduced decomposition implies inertia in the recovery of the system.

The difference between the two sites in Strengbom et al. (2001) concerning vascular plant might be due to the divergence in elapsed time since addition of nitrogen ceased. It is possible that we here see the recovery of vegetation on a time-gradient. Two of the sites in Olsson & Kellner (2006) are located in areas with enlarged deposition of nitrogen caused by human activities. This may cause inertia in the recovery of the system and has to be considered when interpreting the results. However, even if some parameters of nitrogen enrichment appear to recover fast after addition of nitrogen has ceased or relaxed, an ecosystem originally limited by nitrogen seem to have extensive abilities to preserve nitrogen within the system.

13. Synthesis and Discussion

The response on the vegetation of an increased availability of nitrogen by either fertilisation or deposition of anthropogenic origin depends on a set of factors. To what degree the vegetation alters is to a large extent depending on the following aspects:

- Initial composition of the vegetation
- Competitiveness of present species including species in the tree-layer
- Pathogen-host plant interactions
- Possibilities of immigration of species
- Initial pH and change in acidity as a result of the added nutrients

Initial composition of the vegetation is important as well as the position of the dominant species on different gradients relating to their niches. In boreal forests the production capacity (of the dominating tree species) of a certain site can be estimated with some certainty. If the vegetational composition initially is compiled with a mix of species that are co-dominating the forest floor, it is likely that a changed nutrient status will alter the competitive balance between the species. The vegetation will in this case change into one indicating a more productive system. However, if one species is dominating, pathogen-host plant interactions or other disturbances may be initiating the succession. Several studies of nitrogen effects on ground vegetation dominated by one species have been performed. *V. myrtillus* and *C. vulgaris* are species with the possibility of dominating the field-layer. Even though they are adapted to ecosystems limited of nitrogen, these species seem to be competitive also when nitrogen is added to the system. A theory of the causes behind this, hypothesise that ericaceous shrubs are competitive due to their large maximum biomass. Plant-pathogens may however increase due to fertilisation/deposition of nitrogen and alter the competitive balances (figure 1).

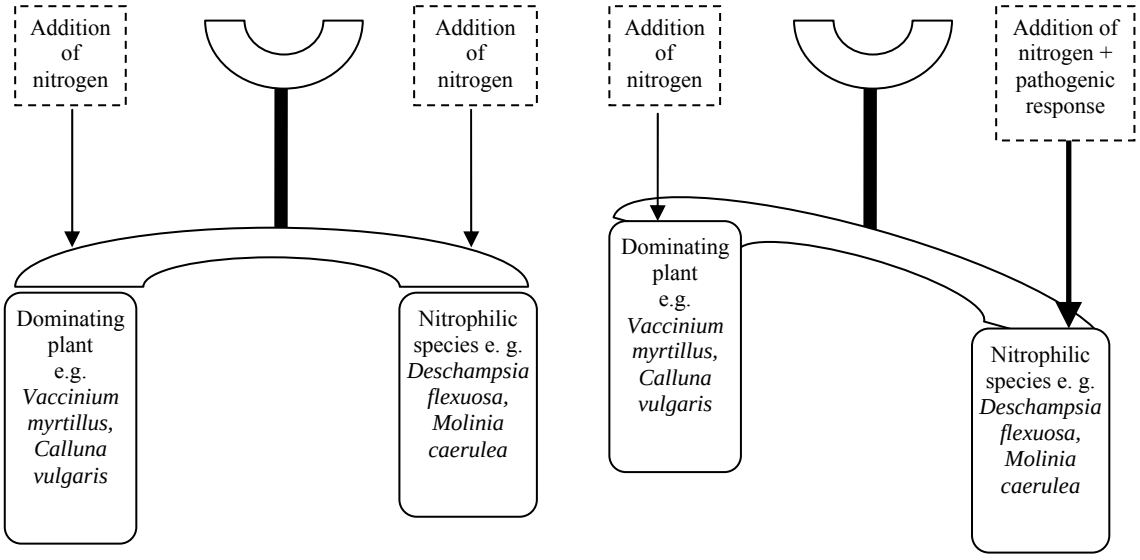

Figure 1. Illustration of altered competitive balance between species in the ground vegetation.

How competitive a plant is when the levels of nutrients in the system are enhanced depends to a large extent on its abilities to utilise the increased resources. If an ecosystem is enriched by nitrogen, the relative and absolute amount of nitrate increases. There are differences between the ability of plants to utilise nitrate for growth, which influence how a plant will perform with the new nutrient status. When a system initially limited by nitrogen gets nitrogen saturated, limitation of other resources occurs. Limitations may arise in other nutrients as well as in light and water. Therefore plants plasticity in relation to other growth resources impacts their competitiveness. In general tall- and fast growing plants are more competitive than their opposites, mainly due to asymmetric competition for light.

The concept of symmetric-asymmetric competition is essential when forecasting the effects of a fertiliser regime on an ecosystem. In general competition for light is considered to be asymmetric, while competition for water and nutrients is symmetric (Weiner 1990; Connolly & Wayne 1996). Boreal and boreo-nemoral ecosystems are mainly limited by nitrogen and symmetric competition can be presumed to play an important role in controlling the composition of the vegetation. As a system gets saturated with nitrogen the competition changes into asymmetric (figure 2).

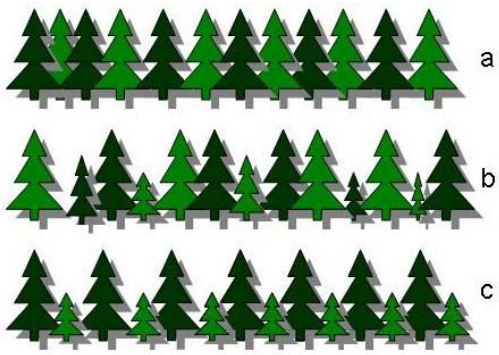

Figure 2. Schematic model of symmetric and asymmetric competition. (a) Symmetric competition, no individual reaches dominance. (b) Asymmetric competition on the individual level, some individuals are more competitive and reach dominance. (c) Asymmetric competition between species. One species is more competitive and reaches dominance. After Freckleton and Watkinson (2001).

Effects of added nitrogen on vegetation can be divided into two main groups depending on when they occur; immediate, and long-term. The immediate effects are caused by the toxicity of nitrogen on plants, especially bryophytes and lichens. The long-term effects are changes through an accumulation of nitrogen in the system, increased competition in the ground vegetation and altered (decreased) insolation as an effect of a closing canopy. If the addition of nitrogen is limited in time and amount, the system tends to recover (figure 3). However, there are large differences between species in time of re-establishment and long-term effects may occur due to a changed competitive balance. Plants adapted to nitrogen limited ecosystems have very often well developed abilities to housekeep nitrogen and recycle it within the system.

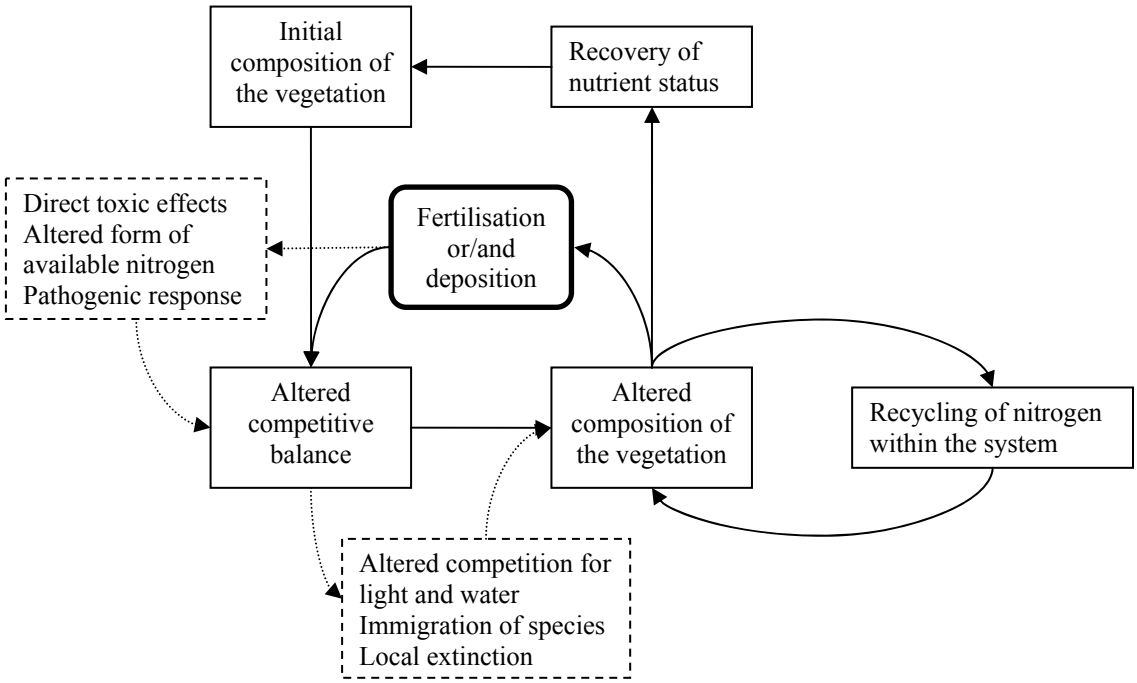

Figure 3. Schematic model of vegetation changes in a nitrogen enriched system.

Forestry of today has a large impact of the composition and extension of the ground vegetation. Clear-cutting of old forest and replacing it with monocultures is changing the light-conditions on the ground. Decreased cover of vegetation when the forest is clear-cut leads to increased temperatures in the soil and thereby increased mineralisation of nitrogen. This favours species that are adapted to early succession stages after large-scale disturbances. When new forest establish, the competition between strata increases. When old forests starts to decline in vitality with increased litterfall, more light is penetrating through the canopy and the ground vegetation can develop. However, shortened rotation periods mean that the time available for plants to recolonise is reduced.

The development of species (plants) richness during the development of a forest stand under a traditional management regime and intensive management is hypothesised in a model developed by Peet and Christensen (1998). This model implies an increase in species richness during the early stages of the rotation period, a decrease during the thinning period when the competition from the tree layer is at its peak, followed by a slowly subsiding increase as the forest ages.

In intensive management with fertilisation starting in juvenile stands, the phase of establishment is shortened, why the species richness can be expected to be lower when it peaks before the thinning period. A more intensive competition for light from the tree canopy during the thinning period may cause a deeper nadir in species richness, especially in forest that normally does not reach a totally closed canopy. Reduced light conditions as an effect of a faster development of the canopy in young fertilised stands

may also lead to a slower increase of species number than in traditional management during the aging phase. The increase of species in this phase is positively related to the intensity of the thinning regime. A management model without thinning would imply the lowest increase of species. The shorter period of establishment together with more intensive competition can lead to enhanced loss of species, especially when this kind of management is applied during repeated rotation periods. This way the silvicultural methods disfavour slow-growing plant species that are adapted to small-scale disturbance regimes. Intensive forestry with fertilisation of monocultures with *P. abies* and shortened rotation periods will enhance these effects. Shorter rotation periods with more frequent clear-cuts may on the other hand lead to an increase in species which are favoured by large-scale disturbances.

The introduction of intensive forestry on a limited part of the forest land may give possibilities to make land-area available for other purposes than forestry. This will however need a change in society's view on the relation forestry/nature conservation and whether or not we should have single-purpose land-use. This can be relied to the always present SLOSS-dilemma (Single Large or Several Small reserves) in nature conservation.

14. Perspectives

There are very few studies dealing with the effects of nitrogen fertilisers on the field vegetation in young forest. There are however a few studies on nitrogen content of the soil and leaching after clear-cut of forest in fertilisation experiments (Ring et al. 2003; Högbom et al. 2001). Ring et al. (2003) concludes that whether or not the vegetation after clear-cut is affected by previous fertilisation, is to a large extent unexplored. One study did not however find any significant changes in biomass production of the ground vegetation after clear-cut (see reference in Ring et al. 2003). Even less work than on clear-cuts is probably done on the effects of fertilisation in young forests. Many studies on the effects of fertilisation in old or middle aged forests, points out the reaction on the canopy closure as one factor, which to large extent determines what happens to the field vegetation. The effect of the canopy on field vegetation is initially missing in clear-cuts and plantations but the importance increase rapidly in young forests when they are fertilised. The effects of fertilisation can thereby be expected to be somewhat different in young open forest than in older stands, where the canopy already from the beginning has a high degree of closure. More research is needed within these fields, both where the effects on field vegetation are studied when fertilised forests are regenerated and fertilisation in young forests.

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